

Efficiency of utilization of various sources of energy for growth

(available energy/energetic efficiency/body fat/Atwater values)

KAREN DONATO* AND D. M. HEGSTED†‡

Department of Nutrition, Harvard School of Public Health, Boston, MA 02115

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ABSTRACT The relative efficiency of dietary sucrose, protein sources, and fats in depositing body protein and fat (total energy) was directly estimated in young rats by feeding graded levels of each as supplements to a fixed amount of a basal diet that was presumably adequate in all essential nutrients except for energy. Under these conditions, the net gain in total body energy was a linear function of the amount of supplement added and the data fulfill the criteria of a valid slope-ratio bioassay. The available energy measured by this technique for sucrose and protein were similar, as would be expected. Dietary fat, however, was a more efficient source of energy. Compared to sucrose with 3.94 kcal/g (1 cal = 4.184 J), the average potency of dietary fat was 11.1 kcal/g, or $\approx 124\%$ of the expected value of 9 kcal/g. Fat supplements increased the deposition of body fat even when total energy intake was severely limited. The Atwater value of 9 kcal per g of fat is not appropriate under these conditions and probably not under other conditions.

The available energy in various foods was estimated by Atwater and Bryant (1) by subtracting the energy lost in urine and feces from the total combustible energy in the food and yielded the familiar Atwater values of 4, 4, and 9 kcal/g (1 cal = 4.184 J) for carbohydrate, protein, and fat. These values obtained by difference, however, assume that all of the material was oxidized in the body, which does not happen during growth and may not happen under various other conditions. As Merrill and Watt (2) note, Atwater did distinguish between physical and physiological fuel values, the latter being defined as "the actual benefit gained by the body from the use of fuel for different purposes." Although specific instances in which physiological fuel values were different from the Atwater values were apparently not identified, this distinction does allow for the possibility that the energy from various fuel sources might not be used with the same efficiency. There is, in fact, a considerable literature (3–8) indicating that the energy from dietary fat is more efficiently utilized than the energy from carbohydrate.

Rice *et al.* (9) suggested that the total energy in various foods available for growth might be estimated by measuring the rate of growth when rats were fed a constant amount of a basal diet adequate to all essential nutrients to which energy supplements were added. Under these conditions, only the energy in the supplement should control the rate of growth. Rice *et al.*, however, assumed that during growth the deposition of body energy would be proportional to the rate of growth, which is not a valid assumption. Hill and co-workers (10–12) estimated the available energy in various chicken rations by the change in total body energy (body protein plus fat) over the test period. They concluded that when fat (corn oil) was isocalorically substituted for glucose, the tissue energy gains were greater with the higher fat rations. Although corn oil contained 8.8 kcal/g (bomb calorimeter

value), it appeared to provide ≈ 10.8 kcal/g, or 124% of the expected value when compared to glucose.

Although the conclusions of Hill *et al.* appear convincing, bioassays of this kind for available energy have not been strictly validated statistically (13). The data presented in this paper demonstrate that the energy available for growth (gain in body energy as measured by gain in body protein and fat) can be quantitated in assays similar to those suggested by Rice *et al.* (9) and that the available energy from dietary fat under these conditions compared to sucrose is substantially larger than predicted from the Atwater values.

METHODS

The design of the four experiments reported was similar to that proposed by Rice *et al.* (9). The three basal diets used (Table 1) were formulated to provide all of the essential nutrients when fed in limiting amounts, so the added energy supplement would be the only variable to affect the rates of weight gain and change in body composition. The weanling male rats of the Charles River strain (Charles River Breeding Laboratories) used in the four experiments received daily 5 g of one of the basal diets to which a fixed amount of the energy supplement under study was added.

In each experiment, groups of animals received graded levels of sucrose. The response of these animals was compared to those that received fat (Spry, Lever Brothers), casein (General Biochemicals), or gluten (General Biochemicals). The amounts of the various supplements provided in the four different experiments are shown in the tables.

After the weanling rats were received in the laboratory, they were fed a laboratory rat chow for 3 days and 5 g of the basal diet for the next 3 days. They were then divided into groups of similar mean weight. Each group in experiments 1 and 2 contained five animals; there were four animals per group in experiments 3 and 4. In each experiment, one group of animals was killed for analysis of body composition. The remaining animals received the appropriate diet for 21 days and were then killed for analysis.[§]

The animals were housed in raised individual cages, kept at a constant temperature and humidity, and weighed two or three times weekly. Papers were placed under the cages so that any spilled food could be weighed and an equivalent amount added to the diet in the next few days. Fortunately, spillage was insignificant.

When the animals were killed, the stomach and cecum were removed and discarded to avoid residual food, and the

*Present address: Nutrition Coordinating Committee, National Institutes of Health, Bethesda, MD 20205.

†Present address: Harvard Medical School, New England Regional Primate Research Center, One Pine Hill Drive, Southborough, MA 01772.

‡To whom reprint requests should be addressed.

§In experiment 3, additional groups were fed the various supplements and were killed after 1 and 2 weeks. The data appear to be similar to those obtained after 3 weeks, but since these studies have not been replicated, they are not presented here.

Table 1. Basal diets

Constituent	Exp. 1	Constituent	Exps. 2 and 3	Exp. 4
Casein, %	43.4	Lactalbumin, %	70.0	66.6
Salt mix,* %	12.0	Salt mix, %	12.0	10.0
Vitamin mix, [†] %	1.2	Vitamin mix, %	1.2	1.0
Spry, [‡] %	7.2	Spry, %	7.2	2.0
Sucrose, %	35.7	Sucrose, %	9.0	19.8
Choline chloride, %	0.5	Choline chloride, %	0.6	0.5

*Prepared as described in ref. 14. Modified by the addition of 0.05 g of sodium selenite and 0.05 g of chromium acetate.

[†]Prepared as described in ref. 15.

[‡]Purchased from Lever Brothers (New York).

carcasses were wrapped in foil and frozen. The carcasses were later chopped into small pieces and dried to constant weight at 95°C in a tared beaker to determine total body water. The beaker and dried carcasses were washed several times with ether to remove most of the body fat, the ether was evaporated, and the fat was weighed. The partially defatted carcass was then ground and a 5-g sample was taken for soxhlet extraction with ether. Total body fat was calculated from the two fat extractions. Two grams of the fat-free dry carcass was digested in ≈90 ml of 18% sulfuric acid and diluted with water to 100 ml to determine total body protein by microkjeldahl technique.

To calculate the change in body energy content of each animal over the 21-day period, the average energy content of the animals killed at the beginning (day 0 controls) was calculated. This value multiplied by the starting weight of

each animal yielded the estimated energy content, which was then subtracted from the determined value at 21 days. Body fat was assumed to contain 9.4 kcal/g and body protein was assumed to contain 4.0 kcal/g. We recognize that the actual energy content of protein approximates 5.6 kcal/g, but the protein content of the basal diet, which all animals received and which does not enter into the calculations, provided sufficient protein for body protein deposition. Thus, it is more logical to assume that the changes in body protein due to energy supplements were the result of the energy content of the supplements. Whatever value is used, however, does not change the relative potency, because differences in body protein were not large in any of the experiments.

The data were evaluated by analysis of variance as described (16, 17), based on the method proposed by Finney (13).

RESULTS

Complete analysis of variance of the data from each experiment is shown in Table 2. The lack of statistical significance for curvature, intersection, and blanks demonstrates that the regression lines do not significantly depart from linearity, have a common intersection, and are similar whether blanks (animals that received no supplement) are included or not. Thus, the assays fulfill the criteria of a valid slope-ratio assay, and the relative energy content of the various supplements can be quantitatively compared.

Table 3 shows the analytical data from experiment 1 and the calculated regression lines are shown in Fig. 1. The *x* axis is the total amount of supplement in grams consumed over the 21-day period (daily supplement × 21). Thus, the slope of the line represents the energy deposition per gram of supplement

Table 2. Analysis of variance

Source of variation	Sum of squares	Mean squares	df	F	P
Experiment 1					
Due to curvature	285.01	142.50	2	0.357	>0.5 NS
Due to intersection	1,156.01	1,156.01	1		≈0.08 NS
Due to blanks	152.03	152.03	1	0.617	>0.50 NS
Due to regression	246,029.95	123,090.99	2	308.8	<0.01
Error without blanks	20,481.37	393.87	52		
Error with blanks		398.61	51		
Total	266,511.32		54		
Experiment 2					
Due to curvature	10,500.32	3,500.11	3	4.02	=0.05 NS
Due to intersection	5,252.41	2,626.20	2	3.02	=0.08 NS
Due to blanks	1,420.97	1,420.97	1	1.28	=0.2 NS
Due to regression	528,105.99	176,508.98	3	202.9	<0.01
Error without blanks	53,621.22	879.04	61		
Error with blanks	52,200.25	870.00	60		
Total	581,727.22		64		
Experiment 3					
Due to curvature	1,804.22	902.11	2	1.46	>0.1 NS
Due to intersection	932.51	932.51	1	1.512	=0.08 NS
Due to blanks	122.19	122.19	1	0.445	=0.5 NS
Due to regression	519,027.81	259,574.99	2	420.8	<0.01
Error without blanks	61,812.01	612.00	101		
Error with blanks	61,689.82	616.89	100		
Total	580,839.82		103		
Experiment 4					
Due to curvature	285.79	142.89	2	0.359	>0.5 NS
Due to intersection	1,153.17	1,153.17	1	2.89	=0.08 NS
Due to blanks	150.27	150.27	1	0.377	>0.5 NS
Due to regression	246,064.24	123,107.25	2	309.1	<0.01
Error without blanks	20,465.01	393.56	52		
Error with blanks	20,314.75	393.33	51		
Total	266,529.26		54		

df, Degrees of freedom; F, variance ratio; NS, not significant.

Table 3. Data on body composition: Experiment 1

Group	Type	Supplement		Body composition			Total calories, ×10 ⁻³	Increment in body energy, [†] kcal
		Amount		Weight, g	Protein, g	Fat, g		
		Daily, g	Total,* g					
1	None	0	0	74.4	14.0	2.41	80.0	3.5 ± 8.8
2	Sucrose	1.5	31.5	95.0	17.9	3.31	104.6	28.1 ± 6.9
3	Sucrose	3.0	63.0	116.9	23.5	4.01	133.9	57.4 ± 6.9
4	Sucrose	4.5	94.5	138.8	28.1	5.86	170.3	93.8 ± 17.2
5	Sucrose	6.0	126.0	152.7	29.2	10.53	218.17	142.2 ± 27.8
6	Sucrose	7.5	157.5	156.6	29.0	15.32	262.9	186.4 ± 24.8
7	Fat (Spry)	0.67	14.1	97.7	18.7	5.61	129.4	52.9 ± 20.8
8	Fat (Spry)	1.34	28.1	118.9	24.8	6.65	164.2	87.7 ± 17.1
9	Fat (Spry)	2.01	42.2	141.8	29.5	8.84	204.9	128.4 ± 12.0
10	Fat (Spry)	2.68	56.3	157.8	31.5	15.20	271.9	195.4 ± 24.7
11	Fat (Spry)	3.35	70.4	171.9	34.4	16.97	300.5	224.0 ± 12.9
12	Day 0 ccntrol			66.8	12.8	2.56	76.5	

*Over 21-day period.

[†]Carcass calories less day 0 control.

consumed. One gram of sucrose produced a net gain of 1.1 kcal whereas 1 g of fat produced a gain of 3.25 kcal. If sucrose provides 3.94 kcal/g, the efficiency of energy deposition was 28% ($1.1/3.94 = 0.28$). One gram of fat produced a net gain of 3.24 kcal and was 2.95 times as effective as sucrose. If sucrose provided 3.94 kcal/g, then the comparative value for fat is 11.6 kcal/g. Alternatively, if dietary fat is assumed to have an energy content of 9 kcal/g, the efficiency of energy deposition from fat was 36% compared to 28% for sucrose.

From an inspection of the body composition data (Table 3), it is apparent that the animals receiving fat supplements deposited more body fat than those receiving sucrose. This was true even when the total energy intake was low and growth was severely limited. For example, the lowest level of fat supplement (0.67 g/day) produced approximately the same weight gain as the lowest level of sucrose supplement (1.5 g/day). Yet the fat-supplemented animals had an average total body fat of 5.61 g compared to 3.31 g in the sucrose-supplemented animals. In all experiments, the greater efficiency of dietary fat is largely, if not entirely, explained by increased deposition of body fat.

In this experiment, the total body protein of the animals receiving sucrose supplements apparently plateaued at ≈ 28.1 g and did not increase as greater supplements were provided.

At increased intakes, there was an apparent shift toward deposition of body fat. Although this did not occur with animals receiving fat supplements, it suggested that the basal diet may have been somewhat limited in protein. The basal diet was modified in the next experiments to provide more protein (Table 1) and failure to deposit protein was not observed in the other experiments. Relative values were similar with all three basal diets.

In experiment 2, sucrose, fat, and a protein (casein) were compared (Table 4 and Fig. 2). It is apparent that body composition and energy deposition were similar with the sucrose and protein supplements. One gram of sucrose produced a net gain of 1.35 kcal, somewhat larger than in the previous experiment. Compared to sucrose, the fat supplements produced a net gain of 9.9 kcal/g.

Experiment 3 compared sucrose, fat, and gluten as a protein source (Table 5 and Fig. 3). Sucrose and gluten produced similar gains of body energy—1.35 and 1.42 kcal/g, respectively. Compared to sucrose, the net available energy from fat was 11.35 kcal/g.[§]

Experiment 4 was similar to experiment 1 except that corn oil was used as a fat source. The net gain of the individual animals is shown in Fig. 4. The apparent available energy content of the fat compared to sucrose was 11.6 kcal/g.

DISCUSSION

The data presented adequately demonstrate that the relative energy content of various supplements in producing gains in

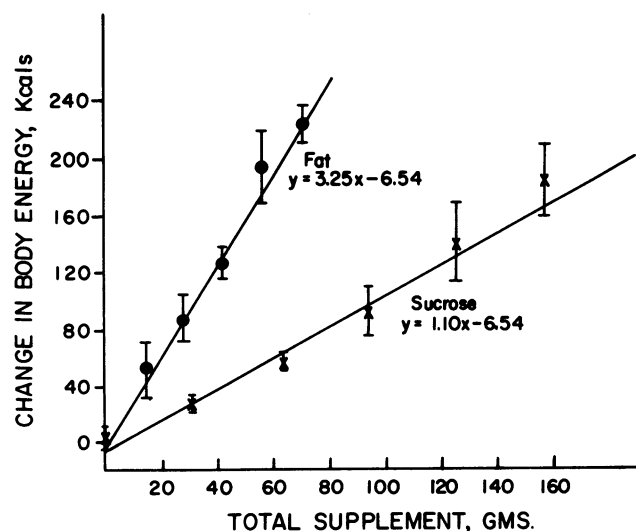


FIG. 1. Change in body energy content with various levels of fat and sucrose supplementation in experiment 1.

Table 4. Changes in body composition: Experiment 2

Group	Type	Supplement			
		Amount, g/day	Increase in calories		
			As fat, kcal	As protein, kcal	Total kcal
1	None	0	1.31	25.97	26.28
2	Sucrose	1.5	15.8	43.2	59.1
3	Sucrose	3.0	42.4	52.7	95.1
4	Sucrose	4.5	60.0	75.6	135.5
5	Sucrose	6.0	67.7	80.0	147.7
6	Sucrose	7.5	129.5	74.2	203.7
7	Fat	1.34	56.7	59.6	116.3
8	Fat	2.67	121.2	75.5	196.7
9	Fat	3.34	132.0	83.7	215.2
10	Casein	3.0	29.2	58.9	88.1
11	Casein	4.5	73.1	68.4	141.5
12	Casein	6.0	95.6	81.7	177.3
13	Casein	7.5	77.6	103.9	181.5

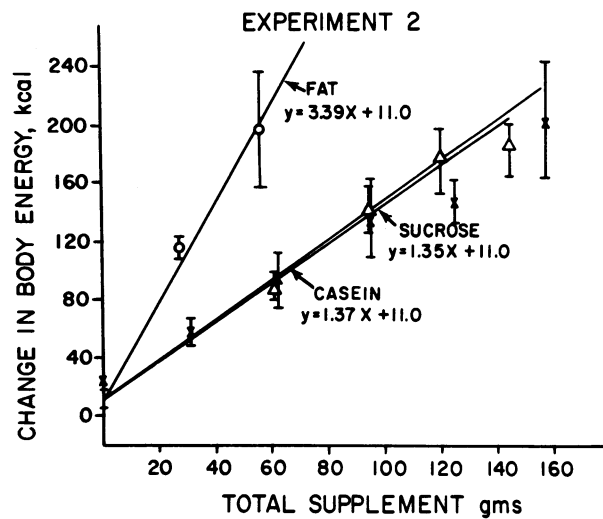


FIG. 2. Change in body energy content with various levels of fat, casein, and sucrose supplementation in experiment 2.

body energy can be validly compared by the technic used. The accuracy of such assays, of course, depends on the number of animals used in each group, the number of groups tested, and the inherent variability in the response of individual animals. It is apparent from the standard deviations of the responses (Table 3) and the differences in individual animals shown in Fig. 4 that there are large differences in the efficiency with which individual animals deposit body energy at equal energy intakes.

In prior experiments, Chu *et al.* (18) compared the change in body composition of Charles River and lean and obese Zucker rats that were fed diets of varying protein content, and the level of protein in the diet determined the food intake and rate of growth. In those studies, the Charles River and lean Zucker rats were $\approx 33\%$ efficient in converting food energy into body energy—a value similar to that reported here. In contrast, the obese strain had an apparent efficiency of $\approx 55\%$. The genetic make-up of the animal plays a major role in determining the efficiency of food utilization, as is also well demonstrated in the animal husbandry literature.

We have deliberately presented the results of these experiments as body energy deposition per gram of supplement rather than the energy content of the supplements. This avoids any assumptions about the metabolizable energy content of the supplements. For comparative purposes, we have used an energy content of sucrose as 3.94 kcal/g, but whatever assumption is made about the energy content of the materials tested does not change the comparative results.

In these experiments, 1 g of sucrose resulted in a net gain

Table 5. Changes in body composition: Experiment 3

Group	Supplement		Increase in calories		
	Type	Amount, g/day	As fat, kcal	As protein, kcal	Total kcal
1	None	0	2.54	24.7	27.2
2	Sucrose	1.5	7.71	51.7	59.4
3	Sucrose	4.5	40.2	88.7	128.9
4	Sucrose	7.5	115.2	94.2	209.4
5	Fat (Spry)	1.34	48.4	56.4	104.8
6	Fat (Spry)	2.67	87.0	92.0	179.0
7	Fat (Spry)	3.34	175.2	100.1	275.3
8	Gluten	1.5	18.1	49.0	67.1
9	Gluten	4.5	45.2	79.1	124.3
10	Gluten	7.5	126.5	87.0	213.5

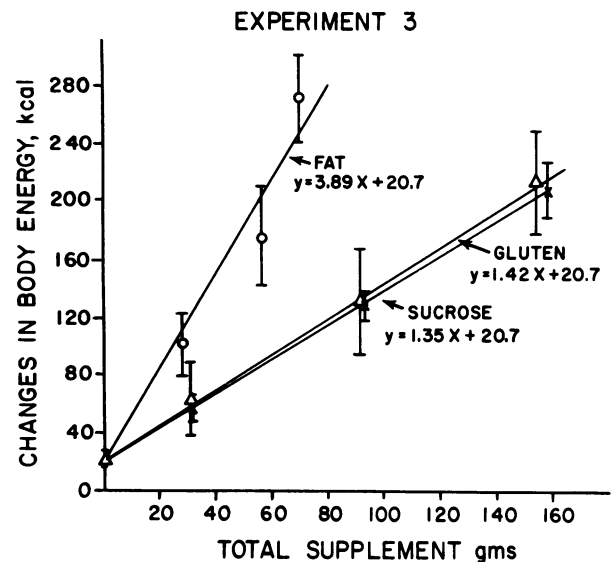


FIG. 3. Change in body energy content with various levels of fat, gluten, and sucrose supplementation in experiment 3.

of body energy of 1.1–1.35 kcal, representing an overall efficiency of 28–34%. The two protein sources tested yield approximately the same values as would be expected from the Atwater values. In contrast, 1 g of fat yielded a net gain of 3.25–3.89 kcal, or an efficiency of 36–43% if fat is assumed to provide 9 kcal of metabolizable energy per g. Compared to sucrose, with an energy content of 3.94 kcal/g, fat provided an average value of 11.1 kcal/g (Table 6). This value confirms the average value reported by Carew and Hill (11) with chickens, which was $\approx 124\%$ of the expected value.

The greater efficiency of dietary fat in these experiments is largely, if not entirely, explained by a greater deposition of body fat when fat supplements were provided. There are many possible explanations (19), but the most likely appears to be that there is a direct conversion of a substantial portion of dietary fat to body fat, even when total energy intake is limited. This is a very energy efficient process compared to the net production of body fat from carbohydrate or protein (20). It is likely that immediately after a meal, when circu-

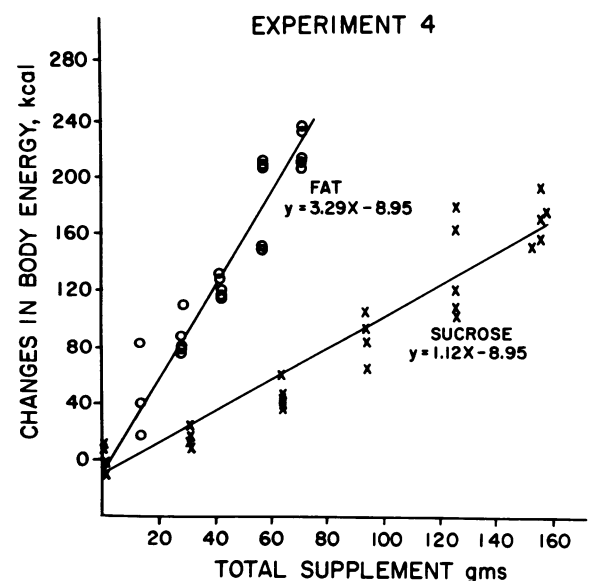


FIG. 4. Change in body energy content with various levels of fat and sucrose supplementation in experiment 4.

Table 6. "Available energy" in fat and protein

Experi- ment	Fat		Protein	
	Source	kcal/g	Source	kcal/g
1	Spry	11.6 (10.6–12.6)		
2	Spry	9.9 (9.0–10.6)	Casein	4.0 (3.7–4.3)
3	Spry	11.4 (10.2–12.6)	Gluten	4.1 (3.7–4.6)
4	Corn oil	11.6 (10.4–13.8)		
Mean		11.1		4.0

Numbers in parentheses represent range.

lating levels of fat are high, that deposition of fat in adipose tissue occurs. Once fat is deposited, it may not be a readily available energy source.

Under these conditions, with growing animals, it is quite clear that the available energy content of a diet cannot be accurately estimated from the usual Atwater values of 4, 4, and 9 kcal of carbohydrate, protein, and fat per g. Whether dietary fat is similarly more efficient under other conditions is not known. In prior work (21) we attempted to compare the effects of restricting diets high in fat, carbohydrate, and protein in relatively obese adult rats. We concluded that loss of body energy was similar with all three diets. In retrospect, however, we note that the animals fed the high fat diet had a body fat content of 30%, compared to an average content of 27% in animals fed diets high in carbohydrate or protein. The results did not reach statistical significance because of the large differences in body composition of individual animals, but the data suggest that, in agreement with the present report, diets high in fat tend to preserve body fat more efficiently, even when total energy intake is severely restricted.

It is quite clear that under some conditions, at least, equal energy intakes, whether measured or calculated from Atwater values, cannot be assumed to be physiologically equivalent. The source of the energy needs consideration. Many nutrition studies utilize the paired-feeding technic in which it is assumed that if total energy intake is equalized, irrespective of the energy source, the effect of energy intake is adequately controlled. This may often not be appropriate. The data also suggest that the fat content of diets may be important in the control or prevention of obesity. This seems particularly relevant, because high fat diets are also known

to promote the development of obesity in experimental animals (22, 23).

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